

Similar diets in two syntopic lizard species (Squamata: Teiidae) from an island in northeastern Argentina

Dietas similares en dos especies sintópicas de lagartijas (Squamata: Teiidae) de una isla del noreste de Argentina

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- Received: 25/Mar/2022
- Accepted: 19/Oct/2022
- Online publishing: 02/May/2023

Citation: Smith LY, Zaracho VH, Arbino MO. 2023. Similar diets in two syntopic lizard species (Squamata: Teiidae) from an island in northeastern Argentina. *Caldasia* 45(2):341–350. doi: <https://doi.org/10.15446/caldasia.v45n2.100682>

ABSTRACT

How coexisting species partition resources is a central focus of ecology, and diet is an important potential axis of competition. Here, we study the diet of syntopic populations of the lizards *Ameivula apipensis* and *Teius oculatus* from an island in northeastern Argentina. Based on stomach contents extracted from specimens collected in September and December 2012 and February 2013, we analyzed prey richness and abundance and calculated both trophic niche breadth and the degree of dietary overlap for the two species. Both species were almost completely insectivorous, and their dietary composition showed a similar prey richness. Numerically, Isoptera dominated the diet of both species, followed by Hymenoptera, insect larvae, and Coleoptera. We report a low niche breadth for each species and substantial overlap between them. This high overlap in their diets could reflect the overall abundance of prey resources in the environment. Other factors, such as the foraging microenvironment and activity period, might be dimensions on which the niches of these species are differentiated.

Keywords. *Ameivula*, Diet, Overlap, *Teius*.

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RESUMEN

Un enfoque central en ecología es el modo en que las especies coexistentes se reparten los recursos, y en este contexto, la dieta es un importante eje potencial de competencia. Aquí, estudiamos la dieta de poblaciones sintópicas de dos especies de lagartijas, *Ameivula apipensis* y *Teius oculatus*, que habitan una isla en el noreste de Argentina. A partir de los contenidos estomacales extraídos de individuos colectados en Septiembre y Diciembre de 2012 y Febrero de 2013, analizamos la riqueza de presas y abundancia y calculamos la amplitud del nicho trófico y el grado de solapamiento para las dos especies. Ambas especies fueron prácticamente insectívoras, y la composición de sus dietas mostró una riqueza de presas similar. Numéricamente, Isoptera dominó la dieta de ambas especies, seguidos por Hymenoptera, larvas de insectos y Coleoptera. Nuestros resultados revelan una amplitud de nicho baja para cada especie y un solapamiento sustancial entre ellas. El alto solapamiento en la dieta de ambas especies probablemente refleja la elevada abundancia en el ambiente de los recursos consumidos. Otros factores, como los microhábitats de forrajeo y el periodo de actividad, podrían ser dimensiones en los cuales los nichos de estas especies están diferenciados.

Palabras clave. *Ameivula*, dieta, solapamiento, *Teius*.

INTRODUCTION

The principle of competitive exclusion proposes that two coexisting species must differ in some aspect of their resource use (Hardin 1960). Ecologists have spent substantial time testing this theory by measuring various niche dimensions, especially those related to food, space, and time (Schoener 1974). In his classical work, Pianka (1973) studied a community of North American lizards and proposed that food is the main dimension on which niches of syntopic species are separated. Diet in lizards is determined by several factors including evolutionary history, body size, microhabitat specialization (or lack thereof), and prey availability (Pianka and Vitt 2003). Lizards can also be classified as sit-and-wait or active foragers based on how they capture their prey. In the sit-and-wait tactic, the lizards move comparatively little and ambush their prey, while in the active foraging tactic the lizards search out and pursue their prey (Vitt and Caldwell 2009). Additionally, lizards can have specialist or generalist diets (Pianka and Vitt 2003).

The lizard family Teiidae includes 172 recognized species that occupy a wide variety of environments (Uetz *et al.*

2022). Species in this family are distributed throughout much of the Western Hemisphere, occurring from Argentina northward into the United States (Goicoechea *et al.* 2016). Like many lizards, teiids are often generalist insectivores (Abdala *et al.* 2004, Montero and Autino 2018). This generalist pattern is evident in dietary studies involving numerous South American teiids, including members of the broadly distributed genera *Ameivula* (Tedesco *et al.* 1995, Dias and Rocha 2007, Santana *et al.* 2010, Sales *et al.* 2012, Freire 2015, Sales and Freire 2015, Menezes *et al.* 2021) and *Teius* (Trivi de Mandri and Chani 1985, Álvarez *et al.* 1988, Acosta *et al.* 1990, 1991, Ávila *et al.* 1992, Cappellari *et al.* 2007, Blanco *et al.* 2012).

In many regions where they occur, teiids are prominent members of lizard communities and multiple species can co-occur in the same habitat. For instance, on Apipé Island in northeastern Argentina, where the present study was done, four of the nine known lizard species belong to this family (Zaracho *et al.* 2014). Two of these teiid species, *Ameivula apipensis*, and *Teius oculatus*, are numerically abundant and occur in syntopy on the island. Trophic studies for both species in syntopy are unknown, and thus Apipé Island represents an excellent site to assess wheth-

er diet structures their coexistence. Additionally, because *A. apipensis* was recently described (Arias *et al.* 2018), many aspects of its natural history including diet remain unknown.

The objective of this work was to study the diet of syntopic populations of *Ameivula apipensis* and *Teius oculatus* lizards from Apipé Island, Corrientes Province, Argentina, to determine if possible dietary differentiation can help explain their coexistence.

MATERIALS AND METHODS

Study area

Apipé Island is located in the Ituzaingó Department, Corrientes Province, Argentina. It lies in the Paraná River immediately downstream of the Yacyretá Dam, and it encompasses 27 710 ha. The island is in a transition zone between the Paranaense and Chacoan phytogeographical provinces, and it is dominated by a subtropical perhumid climate (Thorntwaite 1948). The island's perimeter is almost completely covered with a strip of riparian forest, while the rest of the island supports a variety of habitats including tall grasslands, reed fields, oxbow lakes, and patches of palm savannah restricted to sandy hillocks. Twenty-two vegetation communities have been identified on the island (Fontana 2008). It was previously considered a Natural Reserve (Ley N° 4788/1994), but the protected area was recently reduced to around 10 000 ha and renamed as Parque Provincial Apipé Grande (Ley N° 6568/2021). Thus, the protected area now occupies mainly the central region of the island, which is characterized by two vast lagoons ("lagunas"), and some adjacent riparian forests. Our specific study area was in the western portion of the island, at a site known as Puerto Arazá near the park rangers' quarters (27°29'11"S, 56°56'18"W; datum: WGS 84; 70 m elevation), which is currently outside the limits of the protected area. This site has highly permeable sandy soil grown with a palm savannah dominated by the tall grass *Elionurus muticus* and *Butia yatay* palm trees (Fontana 2008).

Sample collection and processing

We collected all specimens of both *Ameivula apipensis* and *Teius oculatus* as part of a survey of the herpetofauna of the original protected area, in September and December 2012 and February 2013 (Zaracho *et al.* 2014). The collection was authorized under a permit issued by the Reserva

Natural Isla Apipé Grande. We captured lizards by hand from 11:00–13:00 h when both species were active. After capture, we humanely euthanized the lizards using an overdose of a chemical anesthetic (Beaupre *et al.* 2004), in this case, Carticaína-L-Adrenalina, and subsequently fixed them in 10% formalin before preserving them in 70% alcohol. We deposited the preserved specimens in the Colección Herpetológica de la Universidad Nacional del Nordeste (UNNEC): 34 individuals of *A. apipensis* (UNNEC 11722–11732, 11737–11738, 11740, 12723, 12725, 12727, 12732–12735, 12744–12748, 13725–13732) and 17 individuals of *T. oculatus* (UNNEC 11734, 11739, 12728–12731, 12736–12743, 13719–13720, 13724). These specimens consisted of 15 females (snout-to-vent length [SVL]=49.4 ± 11.8 mm [standard deviation], range 31.1–65.2 mm) and 19 males (SVL=52.1 ± 8.1 mm, 36.0–61.9 mm) *A. apipensis* and 8 female (SVL=96.2 ± 5.2 mm, 89.5–102.1 mm), 8 male (SVL=92.8 ± 11.5 mm, 77.2–103.5 mm) and one unsexed juvenile (SVL=46.4 mm) *T. oculatus*. We also dissected the stomachs of two additional *A. apipensis* and one additional *T. oculatus*, but the lizard specimens themselves were accidentally lost. For these three individuals, we itemized the stomach contents but excluded them from regression analyses. For these 36 total specimens of *A. apipensis* and 18 total specimens of *T. oculatus*, we dissected their stomachs and examined the contents via a stereomicroscope. We did not analyze intestine contents due to advanced digestion. We identified most prey items in the stomach contents to Order using standard references (Bolton 1997, Brewer and Arguello 1980, McGavin 2002, Richards and Davies 1984). We used these Order-level identifications as bins for our analyses, with the addition of the conglomerate bin's "larvae" and "nymphs" into which all immature invertebrates were combined. We also identified certain prey items to lower taxonomic levels to obtain supplementary information. For partial remains of prey that we found in the samples, such as incomplete legs, antennae, or jaws, when possible, we identified them using other literature sources (Brothers and Finnamore 1993, Cuezco 1998, Palacio and Fernández 2003, Ocampo 2008, Guzmán de Tomé and Aranda 2008, Grismado *et al.* 2014, Paradell and Cavichioli 2014).

Analyses

We recorded the richness, abundance, frequency of occurrence (i.e., number of lizards containing a given prey item) and volume of each prey item. We calculated volume using the formula of a spheroid (Dunham 1983):

$$V = \frac{4}{3}\pi \left(\frac{a}{2}\right) \left(\frac{b}{2}\right)^2$$

Where a is the length, and b is the width of the prey. We determined the length and maximum width of the prey's body by excluding appendages such as antennae, legs, ovipositors, spines, and other body ornamentation (Parmelee 1999). If prey remains were incomplete, we calculated their approximate original size through comparison with reference prey items of similar body size (Cuevas and Martori 2007). We took measurements under a Leica ES4 stereoscopic microscope using digital calipers with a precision of up to 0.01 mm. For highly digested prey items that were not measurable but which were identifiable to Order, we grouped them as non-measurable (NM). We only considered these highly digested items in terms of number and frequency of occurrence, and we excluded them from subsequent analyses. We consider this exclusion justifiable because NM prey represented a small percentage of total prey items for each species (<5%).

To analyze the relationship between the size of lizard predators and their prey, we performed a regression of the log-transformed data using the highest volume of prey in each stomach as the dependent variable and snout-to-vent length and head width of the lizard as independent variables.

We calculated the relative importance of each prey in the diet based on the absolute importance index (AI) (George and Hadley 1979, Hyslop 1980):

$$RI = 100AI / \sum_1^n AI$$

Where RI = relative importance index, AI (absolute importance index) = % frequency occurrence + % total weight (substituted for % total volumes), and n = number of different prey items.

To establish the hierarchy of the species' diets, we applied a categorization criterion to the RI , which uses the highest value from the index to calculate the percentage of all other values. We categorized prey types as fundamental when their percentage varied between 75–100%, secondary at 50–74%, accessory at 25–49%, and accidental at <25% (Montori 1991).

We based the trophic niche breadth of each species on Levins' index:

$$B = 1 / \frac{1}{\sum p_j^2}$$

Where p_j represents the relative frequency of individuals in the j^{th} category (Levins 1968), which we standardized as $B_s = B - 1 / n - 1$, where n = number of food items (Hurlbert 1978). B_s values vary from 0 (minimum niche amplitude, species consumes a prey type) to 1 (maximum niche amplitude, species exploits available types in equal proportions) (Krebs 1989).

We calculated the degree of dietary overlap between the two lizard species using the overlap coefficient formula (Pianka 1986):

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

Where O_{jk} = Pianka's index of niche overlap between lizard species j and k , and i is the type of resource. Values range from 0 (no overlap) to 1 (total overlap). We categorized overlap values as high (1.00–0.60), medium (0.55–0.25) and low (0.20–0.00) according to Pérez and Balta (2007). We carried out the analysis with EcoSim 7.72 (Gotelli and Entsminger 2004) using the values of the percentage number of the prey. To determine if the observed overlap diverged significantly from a random distribution (absence of overlap), we performed a randomization analysis using the EcoSim program (Gotelli and Entsminger 2003). This program performs Monte Carlo permutations to create "pseudo-communities" (Pianka 1974) and statistically compares the patterns in these pseudo-communities and the actual data matrix.

RESULTS

Thirty-two *A. apipensis* stomachs (88.8%) contained prey. We counted a total of 374 prey items, which we classified into twelve prey types (Table 1). Isoptera were the most numerous prey (67.1%) and had the greatest volume (48.8%). Other abundant prey categories were Hymenoptera, larvae, and Araneae. Insects represented the vast majority

of prey items (91.3%), followed by spiders (4.5%), other items (0.5%), and NM (3.7%). Although Isoptera were the most commonly-consumed prey, they were nonetheless present in only 59.4% of stomachs that contained prey. Hymenoptera prey mostly consisted of ant workers from the subfamilies Myrmicinae, Ectatomminae, Ponerinae, and Formicine, but winged hymenopterans (wasps, bees) were also observed. Lepidoptera were the most frequently found larvae, while larvae of Coleoptera, Diptera, and ants were rare. Members of Araneae included prey from the families Lycosidae and Theridiidae. Hemipteran nymphs were only found in the diet of this species. These were mainly members of the Cicadellidae family with members of Reduviidae found less frequently. NM items represented 3.74% of the total abundance of ingested prey items. Of these, Araneae, Lepidoptera, and Coleoptera remains were identifiable, but the remaining 2.94% could not be assigned to a taxonomic group. "Other items" consisted of two egg sacs, one of them containing a mantid fly (Neuroptera).

Seventeen *T. oculatus* stomachs (94.4%) contained prey. We counted a total of 1500 prey items, almost all of them insects (99.8%), and grouped them into ten prey types (Table 2). As in *A. apipensis*, Isoptera was the most numerically abundant prey (93.7 %) and had the highest proportional volume (41.2%). Hymenoptera (3.3%) and

Coleoptera (1.4%) were the second and third most abundant prey respectively, but Coleoptera represented a high proportion of prey volume (37.8%) due to their comparatively large body sizes. Within Isoptera, we identified individuals belonging to the subfamilies Syntermitinae (*Cornitermes cumulans*), Nasutiterminae (*Nasutitermes* sp.), and Termitinae (*Neocapritermes* sp.). Coleoptera families with higher abundances included Curculionidae and Scarabaeidae, while the least frequently observed were Carabidae and Elateridae. All Hymenoptera prey items were ants, in contrast to *A. apipensis* which also ate wasps and bees. The ant subfamilies Myrmicinae (*Acromyrmex* sp. and *Solenopsis* sp.), Ectatomminae (*Ectatomma* sp.) and Ponerinae (*Anochetus* sp.) were the most common, while Formicinae (*Camponotus* sp.) were scarcer. NM items represented 0.73% of the total abundance of ingested prey items. Of these, Coleoptera (most abundant), Diptera, Hymenoptera, and Araneae remains were identifiable. The remaining 0.13% were unassignable to a taxonomic group.

Both *A. apipensis* and *T. oculatus* showed no correlation between head width (a proxy for mouth width) and prey size (*A. apipensis*: $R^2 = 0.07$, $F_{1-25} = 1.82$, $P = 0.1899$; *T. oculatus*: $R^2 = 0.24$, $F_{1-13} = 3.45$, $P = 0.086$) nor between body length and prey size (*A. apipensis*: $R^2 = 0.07$, $F_{1-25} = 1.2$, $P = 0.2845$; *T. oculatus*: $R^2 = 0.24$, $F_{1-13} = 1.92$, P

Table 1. Composition of the diet of *Ameivula apipensis* (n = 32 individuals) from Apipé Island, Corrientes Province, Argentina.

Prey item	N (%)	V (%)	F (%)	IRI	JD	Category
Insecta						
Isoptera	251 (67.1)	973.59 (48.8)	19 (59.4)	39.84	100	Fundamental
Diptera	7 (1.9)	55.37 (2.8)	4 (12.5)	3.89	9.78	Accidental
Hymenoptera	35 (9.4)	98.94 (5.0)	10 (31.25)	10.36	25.99	Accessory
Coleoptera	5 (1.3)	50.11 (2.5)	4 (12.5)	3.72	9.33	Accidental
Neuroptera	1 (0.3)	48.56 (2.4)	1 (3.1)	1.32	3.33	Accidental
Hemiptera	3 (0.8)	7.60 (0.4)	3 (9.4)	2.40	6.02	Accidental
Orthoptera	1 (0.3)	195.43 (10.0)	1 (3.1)	2.99	7.52	Accidental
Larvae	25 (6.7)	285.87 (14.3)	15 (46.9)	15.43	38.73	Accessory
Nymphs	13 (3.5)	33.77 (1.7)	7 (21.9)	6.15	15.43	Accidental
Arachnida						
Araneae	17 (4.5)	101.07 (5.1)	13 (40.6)	11.42	28.66	Accessory
Other (egg sac)	2 (0.5)	145.08 (7.8)	1 (3.1)	2.49	6.24	Accidental
NM	14 (3.7)		9 (28.1)			
Total	374	1995.4				

N: number, V: volume (mm³) and F: frequency (absolute values are given, and percentage values in parentheses); IRI: relative importance index; JD: diet hierarchy, (%). NM: not measurable.

= 0.1895). According to RI, Isoptera was the fundamental category for both species. Insect larvae, Araneae and Hymenoptera in *A. apipensis*, and Coleoptera and Hymenoptera in *T. oculatus*, were categorized as accessory items, respectively (Table 1–2).

Levin's index values indicate that the trophic niche breadth of *A. apipensis* ($B_s = 0.1$) and *T. oculatus* ($B = 0.02$) are low. The Pianka index revealed a high overlap in the trophic niches of *A. apipensis* and *T. oculatus* ($O_{jk} = 0.72$), and this overlap was higher than expected by chance: $O_{jk} = 0.63$, P [observed \geq expected] < 0.04 ; P [observed \leq expected] = 0.96.

DISCUSSION

Here we provide the first data on the diet of *A. apipensis*, and termites were both the most numerically abundant prey and the most important prey type by volume in this species. These findings are broadly consistent with the substantial pre-existing dietary data for closely related teiids. Termites were the most important dietary component for *A. abalosi* from the semi-arid Chaco of Argentina (Tedesco *et al.* 1995) and for *A. ocellifera* from the Brazilian Caatinga (Freire 2015). Furthermore, our dietary data for *A. apipensis* was remarkably similar to that of a second population of *A. ocellifera* from a littoral area of Bahía, Brazil (Dias and Rocha 2007) for which termites, larvae, and spiders dominated the diet—just as in our study population of *A. apipensis*. Termites were also recovered as a primary dietary component for the teiid lizard *Glaucomastix littoralis* from a coastal area of Rio de Janeiro, Brazil (Teixeira-Filho *et al.* 2003), and as a secondary dietary component for *G. abaetensis* (with larvae being the dominant prey type) (Dias and Rocha 2007). This latter result is somewhat surprising given that this population of *G. abaetensis* is sympatric with the population of *A. ocellifera* from the littoral area of Bahía, Brazil mentioned earlier. The authors suggest that differences in microhabitat usage or body size could facilitate the coexistence of those two sympatric species. *Ameivula ocellifera* also seems to be capable of dietary plasticity because larvae and pupae dominate the diet of other populations from the Caatinga (Sales *et al.* 2012, Sales and Freire 2015) while populations from a different littoral areas in Paraiba, Brazil consume mainly orthopterans and coleopterans (Santana *et al.* 2010). According to Santana *et al.* (2010), the floristic assemblage and soil composition of the littoral area in

Paraiba seems incapable of supporting termites or the larval phase of various insect groups. More recently, Menezes *et al.* (2021) studied the diet of five teiid species from the Brazilian restinga: *Ameivula ocellifera*, *A. nativo*, *Glaucomastix abaetensis*, *G. littoralis*, and *Contomastix laceroides*. Unsurprisingly, for most of these populations, their diet consisted predominantly of larvae and/or termites.

Turning to our second study species, *T. oculatus*, termites were also the most numerically and volumetrically important dietary component for our study population. This result echoes previous trophic studies for this species from the Sierras de Córdoba in Argentina (Acosta *et al.* 1991) and grasslands in Rio Grande do Sul, Brazil (Cappellari *et al.* 2007). Detailed analysis of the Córdoba populations in two different years also revealed high consumption of Coleoptera (beetles) during the first summer and high consumption of termites and Orthoptera (grasshoppers) in the following summer (Acosta *et al.* 1991). Similarly high dietary consumption of beetles has been documented for populations of *T. oculatus* from northeastern Argentina (Álvarez *et al.* 1988). Beetles and Hymenoptera (ants) were also accessory items in the diet of our study population of *T. oculatus*. In comparison, for *T. oculatus* from Rio Grande do Sul (Brazil), Orthoptera were the most important prey type by volume overall, although termites were the most numerically abundant prey specifically in juveniles and adult males, while ants were the most abundant prey in adult females (Cappellari *et al.* 2007). Among congeneric lizards, high dietary consumption of beetles was reported for *T. teyou* from northeastern Argentina (Álvarez *et al.* 1988), while termites were the dominant dietary item in *T. teyou* populations from the Chaco of Argentina (Trivi de Mandi and Chani 1985) and in *T. suquiensis* in montane environments of Córdoba province, Argentina (Acosta *et al.* 1990). In a separate study of *T. suquiensis*, the consumption of coleopterans, locusts, and larvae was also common, and consumption of locusts was higher during the second study year that corresponded to wetter conditions (Ávila *et al.* 1992). Based on these examples, termites seem to be consistently important in the diet of both *T. oculatus* and other *Teius* species, with beetles, ants, and grasshoppers also representing meaningful dietary components in certain areas or at certain times. Overall, the specific diet of *T. oculatus* seems to vary both geographically and seasonally, with its diet depending on environmental resource availability and, indirectly, on environmental conditions.

Table 2. Composition of the diet of *Teius oculatus* (n = 17 individuals) from Apipé Island, Corrientes Province, Argentina.

Prey item	N (%)	V (%)	F (%)	IRI	JD	Category
Insecta						
Isoptera	1406 (93.7)	4258.9 (41.2)	14 (82.3)	46.25	100	Fundamental
Coleoptera	21 (1.4)	3898.7 (37.8)	10 (58.8)	20.85	45.08	Accessory
Hymenoptera	49 (3.26)	1132.2 (11)	12 (70.6)	18.05	39.02	Accessory
Neuroptera	1 (0.06)	48.8 (0.5)	1 (5.9)	1.36	2.95	Accidental
Odonata	2 (0.13)	202.6 (2)	2 (11.8)	2.94	6.37	Accidental
Blattodea	1 (0.06)	58.7 (0.6)	1 (5.9)	1.38	2.99	Accidental
Orthoptera	1 (0.06)	480.4 (4.6)	1 (5.9)	2.26	4.88	Accidental
Larvae	6 (0.4)	231.4 (2.2)	4 (23.5)	2.57	12.04	Accidental
Arachnida						
Araneae	2 (0.13)	12.9 (0.1)	1 (5.9)	1.31	2.82	Accidental
NM	11 (0.73)					
Total	1500	10324.4				

N: number; V: volume (mm³); F: frequency (absolute values are given, and percentage values in parentheses); RI: relative importance index; JD: diet hierarchy; NM: not measurable.

We found no correlations between lizard size (snout-to-vent length and head width) and prey volume for *A. apipensis* or *T. oculatus*. However, previous studies have reported positive correlations between lizard head width and prey volume, as well as between body length and prey volume (Cappellari *et al.* 2007, Freire 2015, Menezes *et al.* 2021). The absence of a size correlation in both species is thus somewhat of a paradox, and this result could be due to the high consumption of prey that have a low size variation (termites in this case), as has already been hypothesized for other teiid species (Menezes *et al.* 2021). This result could also be related to the specialist tactic, because when a lizard predator selects small prey (e.g., social insects like termites) prey size is not limited by the lizard size, although they can sometimes ingest larger prey (Pianka and Vitt 2003).

The low niche breadths that we calculated for the diets of *A. apipensis* and *T. oculatus* in our study area suggest that these species, at least seasonally, are dietary specialists. An alternative explanation, however, is that these low niche breadths are due to the high availability of a few desirable prey types (López *et al.* 2009). Similarly, although both lizard species consumed essentially identical prey types, with a comparable dominance of termite prey, they may not necessarily be competing for food resources because competition can occur only over scarce sources (Colwell and Futuyma 1971). Where we collected the lizards, termite nests were remarkably abundant on the landscape. Al-

though we did not estimate their nest density, we consider it plausible that the numerical and volumetric dominance of termites in the diet of both of our lizard study species could be attributable to these insects being a high-quality and non-limiting food resource at our study site.

Future trophic studies that account for temporal and fine-scale patterns in lizard foraging and prey availability, as well as research that includes other lizard species present on the island, will provide a more complete view of possible interactions within the lizard community of Apipé Island. Because much of the island is subjected to periodic burns to control vegetation, we also recommend including fire in future studies as another factor that could affect diet composition.

CONCLUSION

On Apipé Island, the diet of *Ameivula apipensis* and *Teius oculatus* specimens collected in September, December and February consisted almost exclusively of insects. Termites, beetles, ants, and insect larvae together comprised nearly the entire diet of both species, albeit in somewhat different numerical abundances and percentages of total prey volume. Of these prey items, termites are the major component of the diet of both species. These results are broadly consistent with those of previous dietary studies of *T. oculatus*, of other *Teius* and *Ameivula* spp., and of related lizard genera in South America. The similar diets

of these two species, at least at certain times of the year, do not appear to limit their coexistence at this site. Future work is necessary to evaluate if their niches are differentiated along other dimensions such as foraging microenvironment or activity period.

AUTHORS' CONTRIBUTION

LYS and VHZ designed the study, performed the analyses, and wrote the early and final version of the manuscript; VHZ collected lizards in the field; LYS and MOA analyzed the stomach contents and identified the prey items; MOA participated in the final corrections of the manuscript.

ACKNOWLEDGMENTS

F. Abreliano, M. Ibarra Polessel, M. Ingaramo, S. Díaz, M. Duré, A. Kehr, and M. Ortiz contributed significantly to this work through data analysis, prey identification, and sharing constructive comments on the manuscript. Two anonymous reviewers provided comments that helped to improve the final version of the manuscript. Financial support was provided by the Universidad Nacional del Nordeste (16Fo12-SGCYT-UNNE).

CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

LITERATURE CITED

- Abdala V, Montero R, Moro S. 2004. Lagartos y anfibios del Litoral Fluvial argentino y áreas de influencia. Estado de conocimiento. In: Aceñolaza FG, editor. *Temas de la Biodiversidad del Litoral Fluvial Argentino*. San Miguel de Tucumán: INSUGEO 12. p. 303–336.
- Acosta JC, Ávila L, Martori RA. 1990. Alimentación de *Teius suquiensis* y *Teius oculatus* en el centro de Argentina I. Composición de la dieta y variación anual. *Bol. Asoc. Herpet. Arg.* 7(1):3.
- Acosta JC, Ávila LJ, Martori RA. 1990. Ecología trófica de *Teius oculatus* (Sauria: Teiidae) en el sur de la Provincia de Córdoba (Argentina): composición, variación anual y estacional de la dieta. *Cuad. Herpetol.* 6(3):12–22.
- Álvarez BB, Tedesco ME, Torales G, Porcel E. 1988. Comportamiento alimentario de dos especies de *Teius* (Lacertilia, Teiidae) del nordeste argentino. *Acta Zool. Lillo.* 41:263–269.
- Arias FJ, Recoder R, Álvarez BB, Ethcepare E, Quipildor M, Lobo F, Rodrigues MT. 2018. Diversity of teiid lizards from Gran Chaco and Western Cerrado (Squamata: Teiidae). *Zool. Scr.* 47:144–158. doi: <https://doi.org/10.1111/zsc.12277>
- Ávila LJ, Acosta JC, Martori RA. 1992. Composición, variación anual y estacional de la dieta de *Teius suquiensis* (Sauria: Teiidae) de la provincia de Córdoba (Argentina). *Cuad. Herpetol.* 7(2):5–13.
- Beaupre SB, Jacobson ER, Lillywhite HB, Zamudio K. 2004. *Guidelines for use of live amphibians and reptiles in field and laboratory research (Second Edition)*. Revised by the Herpetological Animal Care and Use Committee (HACC) of the American Society of Ichthyologists and Herpetologists, Lawrence, Kansas, USA.
- Blanco G, Acosta JC, Piaggio L, Nieva R, Victorica A, Castillo G. 2012. Saurofagia y canibalismo en dos especies de lagartos del centro-oeste de Argentina. *Cuad. Herpetol.* 26(2):91–93.
- Bolton B. 1997. *Identification Guide to the Ant Genera of the World*. Cambridge, Massachusetts, London: Harvard University Press.
- Brewer M, Arguello N. 1980. *Guía ilustrada de insectos comunes de la Argentina*. San Miguel de Tucumán: Ministerio de Cultura y Educación y Fundación Miguel Lillo. Miscelánea 67
- Brothers DJ, Finnamore AT. 1993. Superfamily Vespoidea. In: Goulet H, Ruber JT, editors. *Hymenoptera of the world: an identification guide to families*. Ottawa: Agriculture Canada. p. 161–232.
- Cappellari LH, de Lema T, Prates Jr P, Rocha CFD. 2007. Diet of *Teius oculatus* (Sauria, Teiidae) in southern Brazil (Dom Feliciano, Rio Grande do Sul). *Iheringia, Sér. Zool.* 97(1):31–35. doi: <https://doi.org/10.1590/S0073-47212007000100006>
- Colwell RK, Futuyma DJ. 1971. On the measurement of niche breadth and overlap. *Ecology* 52(4):567–576. doi: <https://doi.org/10.2307/1934144>
- Cuevas MF, Martori R. 2007. Diversidad trófica de dos especies sintópicas del género *Leptodactylus* (Anura: Leptodactylidae) del sudeste de la provincia de Córdoba, Argentina. *Cuad. Herpetol.* 21(1):7–19.
- Cuezzo F. 1998. Formicidae. In: Morrone JJ, Coscarón S, editors. *Biodiversidad de artrópodos argentinos*. Buenos Aires: Ediciones SUR. p. 452–462.
- Dias EJR, Rocha CFD. 2007. Niche differences between two sympatric whiptail lizards (*Cnemidophorus abaetensis* and *C. ocellifer*, Teiidae) in the restinga habitat of northeastern Brazil. *Braz. J. Biol.* 67(1):41–47. doi: <https://doi.org/10.1590/s1519-69842007000100006>
- Dunham AE. 1983. Realized niche overlap, resource abundance and intensity of interspecific competition. In: Huey RD, Pianka ER, Schoener TW, editors. *Lizards Ecology*. Cambridge, Massachusetts and London: Harvard University Press. p. 261–280. doi: <https://doi.org/10.4159/harvard.9780674183384.c15>

- Fontana JL. 2008. Vegetación y diversidad de ambientes en la Reserva Natural Isla Apipé Grande, Provincia de Corrientes, Argentina. In: Aceñolaza FG, editor. *Temas de la Biodiversidad del Litoral Fluvial Argentino III*. San Miguel de Tucumán: INSUGEO. Miscelánea 17. p. 407–424.
- Freire Costa CJ. 2015. Reprodução e dieta do lagarto *Cnemidophorus ocellifer* em uma área de restinga do Nordeste Brasileiro. [Tesis]. [Brasil]: Universidade Federal do Rio Grande do Norte.
- George EL, Hadley WF. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and small mouth bass (*Micropterus dolomieu*) young of the year. *Trans. Am. Fish. Soc.* 108(3):253–257. doi: [https://doi.org/10.1577/1548-8659\(1979\)108%3C253:FAHPBR%3E2.o.CO;2](https://doi.org/10.1577/1548-8659(1979)108%3C253:FAHPBR%3E2.o.CO;2)
- Goicoechea N, Frost DR, De la Riva I, Pellegrino KCM, Sites J, Rodrigues MT, Padial JM. 2016. Molecular systematics of teioid lizards (Teioidea/Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similarity-alignment. *Cladistics* 32:624–671. doi: <https://doi.org/10.1111/cla.12150>
- Gotelli NJ, Entsminger GL. 2003. Swap algorithms in null model analysis. *Ecology* 84(2):532–535. doi: [https://doi.org/10.1890/0012-9658\(2003\)084\[0532:SAINMA\]2.o.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0532:SAINMA]2.o.CO;2)
- Gotelli NJ, Entsminger GL. 2004. EcoSim: Null models software for ecology, Version 7.0. [Last accessed: 20 Jul 2022]
- Grismado CJ, Ramírez MJ, Izquierdo MA. 2014. Araneae: taxonomía, diversidad y clave de identificación de familias. In: Roig-Juñent S, Claps LE, Morrone JJ, editors. *Biodiversidad de artrópodos argentinos*. San Miguel de Tucumán: INSUGEO. Vol. 3. p. 55–93.
- Guzmán de Tomé M, Aranda S. 2008. Elateridae. In: Claps LE, Debandi G, Roig-Juñent S, editors. *Biodiversidad de artrópodos argentinos*. Buenos Aires: Editorial Sociedad Entomológica Argentina. Vol. 2. p. 563–573.
- Hardin G. 1960. The competitive exclusion principle. *Science* 131(3409):1292–1297. doi: <https://doi.org/10.1126/science.131.3409.1292>
- Hurlbert SH. 1978. The measurement of niche overlap and some relatives. *Ecology* 59(1):67–77. doi: <https://doi.org/10.2307/1936632>
- Hyslop EJ. 1980. Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17(4):411–429. doi: <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>
- Krebs C. 1989. *Ecological methodology*. New York: Harper and Row.
- Levins R. 1968. *Evolution in changing environments*. Princeton, New Jersey: Princeton University Press.
- López JA, Scarabotti PA, Medrano MC, Ghirardi R. 2009. Is the red spotted green frog *Hypsiboas punctatus* (Anura: Hylidae) selecting its preys? The importance of prey availability. *Rev. Biol. Tropical* 57(3):847–857. doi: <https://doi.org/10.15517/rbt.v57i3.5497>
- McGavin GC. 2002. *Entomología esencial*. Barcelona: Ariel Ciencia.
- Menezes VA, Amaral V, Souza VV, Rocha CFD. 2021. Variation in feeding ecology of five cnemidophorine lizard species along Brazilian eastern coast. *Cuad. Herpetol.* 35(1): 53–76.
- Montero R, Autino AG. 2018. *Sistemática y filogenia de los vertebrados con énfasis en la fauna argentina*. Third Edition. San Miguel de Tucumán: Editorial independiente.
- Montori A. 1991. Alimentación de los adultos de *Euproctus asper* (Dugés, 1852) en la montaña media del Prepirineo catalán (España). *Rev. Esp. Herpetol.* 5:23–36.
- Ocampo FC. 2008. Scarabaeoidea. In: Claps LE, Debandi G, Roig-Juñent S, editors. *Biodiversidad de artrópodos argentinos*. Mendoza: Editorial Sociedad Entomológica. Vol. 2. p. 495–500.
- Palacio EE, Fernández F. 2003. Claves para las subfamilias y géneros. In: Fernández F, editor. *Introducción a las hormigas de la región Neotropical*. Bogotá: Instituto Humboldt. p. 230–260.
- Paradell S, Cavivhiol R. 2014. Hemiptera: Cicadellidae. In: Roig-Juñent SA, Claps LE, Morrone JJ, editors. *Biodiversidad de Artrópodos argentinos*. San Miguel de Tucumán: INSUGEO. Vol. 3. p. 350–355.
- Parmelee JR. 1999. Trophic ecology of a tropical anuran assemblage. *Scientific Papers, Natural History Museum, University of Kansas* 11:1–59. doi: <https://doi.org/10.5962/bhl.title.16167>
- Pérez J, Balta K. 2007. Ecología de la comunidad de saurios diurnos de la Reserva Nacional de Paracas, Ica, Perú. *Rev. Per. Biol.* 13(3):169–176. doi: <https://doi.org/10.15381/rpb.v13i3.2334>
- Pianka ER. 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4:53–74. doi: <https://doi.org/10.1146/annurev.es.04.110173.000413>
- Pianka ER. 1974. Niche overlap and diffuse competition. *Proc. Natl. Acad. Sci. USA.* 71(5):2141–2145. doi: <https://doi.org/10.1073/pnas.71.5.2141>
- Pianka ER. 1986. *Ecology and natural history of desert lizards. Analyses of the ecological niche and community structure*. New Jersey: Princeton University Press. doi: <https://doi.org/10.1515/9781400886142>
- Pianka ER, Vitt LJ. 2003. *Lizards: Windows to the Evolution of Diversity*. Berkeley: University of California Press. doi: <https://doi.org/10.1525/california/9780520234017.001.0001>
- Richards OW, Davies RG. 1984. *Tratado de entomología IMMS: clasificación y Biología*. Barcelona: Ediciones Omega S.A. Vol. 2.
- Sales RFD, Freire EMX. 2015. Diet and foraging of *Ameivula ocellifera* (Squamata, Teiidae) in the Brazilian semiarid Caatinga. *J. Herpetol.* 49(4):579–585. doi: <https://doi.org/10.1670/14-041>
- Sales RFD, Ribeiro LB, Jorge JS, Freire EMX. 2012. Feeding habits and predator-prey size relationships in the whiptail lizard *Cnemidophorus ocellifer* (Teiidae) in the semiarid region of Brazil. *S. Am. J. Herpetol.* 7(2):149–156. doi: <https://doi.org/10.2994/057.007.0204>

- Santana GG, Vasconcello A, Gadelha YEA, Vieira WLS, Almida WO, Nóbrega RP, Alves RRN. 2010. Feeding habits, sexual dimorphism and size at maturity of the lizard *Cnemidophorus ocellifer* (Spix, 1825) (Teiidae) in a reforested resting habitat in northeastern Brazil. *Braz. J. Biol.* 70(2):409–416. doi: <https://doi.org/10.1590/S1519-69842010005000006>
- Schoener TW. 1974. Resource partitioning in ecological communities. *Science* 185(4145):27–39. doi: <https://doi.org/10.1126/science.185.4145.27>
- Tedesco ME, Torales G, Porcel E. 1995. Aportes al conocimiento de la dieta de *Cnemidophorus ocellifer* (Squamata, Teiidae). *FACENA* 11:19–23.
- Teixeira-Filho PF, Rocha CFD, Ribas SC. 2003. Relative feeding specialization may depress ontogenetic, seasonal, and sexual variations in diet: the endemic lizard, *Cnemidophorus littoralis* (Teiidae). *Braz. J. Biol.* 63(2):321–328. doi: <https://doi.org/10.1590/S1519-69842003000200017>
- Trivi de Mandri M, Chani J. 1985. Estudio preliminar sobre los hábitos alimentarios de *Teius teyou*, Muller, 1928 (Lacertilia, Teiidae). *Bol. Asoc. Herpet. Arg.* 2(1–2):6–7.
- Thorntwaite, CW. 1948. An approach toward a rational classification of climate. *Geog. R.* 38(1):55–94. doi: <https://doi.org/10.2307/210739>
- Uetz P, Freed P, Aguilar R, Reyes F, Hošek J. 2022. The Reptile Database. [Last accessed: 25 Sep 2022].
- Vitt LJ, Caldwell JP. 2009. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. Third Edition. Burlington, Massachusetts, USA: Academic Press. doi: <https://doi.org/10.1016/B978-0-12-374346-6.00002-X>
- Zaracho VH, Ingaramo MDR, Semhan RV, Etchepare EG, Acosta JL, Falcione AC, Álvarez BB. 2014. Herpetofauna de la Reserva Natural Provincial Isla Apipé Grande (Corrientes, Argentina). *Cuad. Herpet.* 28:153–160.